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Photophysiology of nitrate limited phytoplankton communities in Kongsfjorden, Spitsbergen

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Abstract

In Arctic coastal regions, the phytoplankton bloom is often initiated by meltwater induced stratification in spring, while subsequent nutrient depletion is believed to drive phytoplankton succession in summer. The associated changes in photophysiology are difficult to identify, because these can be governed by acclimation to light and nutrient availability as well as variations in phytoplankton biomass and taxonomic composition. In the present study, the consequences of nutrient limitation for photophysiology and growth were assessed in natural phytoplankton communities from Kongsfjorden, Spitsbergen. A series of nutrient addition experiments demonstrated N-limitation from mid-June onwards and possible co-limitation with P later in summer. The onset of N-limitation was associated with a pronounced change in taxonomic composition from a dictyochophytes to a haptophytes dominated community. Fast Repetition Rate fluorometry measurements of photosystem II (PSII) photophysiology showed that the dictyochophytes dominated community was characterized by high PSII efficiency and electron transport rates which were efficiently used for growth. Marked changes in PSII photophysiology were observed later in summer, with decreasing efficiencies, lower connectivity between reaction centers, and slower turnover rates. Simultaneously, alternative electron requirements downstream of PSII became more important and energy was likely allocated to the uptake of nutrients rather than carbon fixation and growth. Relief of nutrient limitation during the nutrient addition experiments did not lead to pronounced changes in PSII photophysiology. It is, therefore, concluded that PSII photophysiology of the phytoplankton community in Kongsfjorden is associated with changes in species composition rather than a direct effect of nutrient availability or nutrient limitation.

Springtime phytoplankton growth conditions in ice-free coastal regions of the Arctic are strongly governed by oceanic as well as glacial influences (Hodal et al. 2012; Carmack et al. 2016; Van de Poll et al. 2016). The phytoplankton bloom is initiated by meltwater induced stratification in spring, while the subsequent depletion of nutrients from surface waters is believed to be a driving factor in phytoplankton succession (Strom et al. 2006; Iversen and Seuthe 2011; Van de Poll et al. in press). Low nitrogen to phosphate (N : P) ratios suggest that nitrogen is the main limiting nutrient in coastal Arctic regions (Strom et al. 2006; Piquet et al. 2014; Van de Poll et al. 2016) and in the Arctic at large (Popova et al. 2010). Yet, (co-)limitation by other nutrients cannot be excluded when nitrogen is regenerated toward the end of the phytoplankton

bloom period (Van de Poll et al. 2016). The availability of nutrients not only drives phytoplankton biomass, but also the taxonomic composition with diatoms typically dominating the phytoplankton community in spring and small nano- and pico-phytoplankton species throughout summer (Strom et al. 2006; Li et al. 2009; Piquet et al. 2014). During this period, diatoms are likely limited by relatively low silicate concentrations (Piquet et al. 2014; Van de Poll et al. 2016). Despite the importance of nutrient availability in phytoplankton biomass and taxonomic composition, photophysiology and primary production are not always directly related to environmental conditions in the Arctic (Strom et al. 2006; Palmer et al. 2011; Van de Poll et al. in press).

In natural phytoplankton communities, changes in photophysiological parameters are difficult to ascribe to acclimation of specific phytoplankton species in response to environmental conditions or to variations in photophysiology among taxonomic groups (Suggett et al. 2009). Detailed laboratory studies with single phytoplankton species have revealed that both nutrient starvation and limitation may have considerable effects on

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phytoplankton photophysiology. Generally, the light harvesting capacity is reduced during nutrient starvation by a reduction in the cellular chlorophyll *a* (Chl *a*) concentration and quantum yield of photosystem II (PSII) (F_v/F_m), as well as an increase in the relative amount of photoprotective carotenoids per Chl *a* (XC/Chl *a*) and subsequent nonphotochemical quenching processes (NPQ_{NSV}) (Geider et al. 1993, 1998; Berges et al. 1996; Kulk et al. 2013). However, Chl *a* specific absorption and the absorption cross section of the remaining PSII (σ_{PSII}) may increase during nutrient starvation (Kolber et al. 1988; Geider et al. 1993; Berges et al. 1996), partially counteracting the reduced light harvesting capacity. Moreover, nutrient starvation affects photochemical energy conversion by a decrease in photosynthetically important proteins such as D1 and Rubisco (Geider et al. 1993; Steglich et al. 2001), while energy derived from the light reactions of photosynthesis may be used for the rapid uptake of nutrients at the expense of carbon fixation (Beardall et al. 2001). Many of these short-term stress related variations in photophysiology appear to decrease as phytoplankton acclimate to low nutrient availability over longer periods of time (Cullen et al. 1992; Parkhill et al. 2001; Suggett et al. 2009). Such acclimation to nutrient limitation could explain the difficulty to relate photophysiology and primary production to environmental conditions in coastal Arctic regions, as has also been observed in low nutrient open-ocean regions (Marañón 2005; Moore et al. 2008; Suggett et al. 2009).

The question arises whether changes in photophysiology and primary production in Arctic phytoplankton communities are directly related to physiological acclimation in response to nutrient starvation and/or limitation or are driven by changes in phytoplankton biomass and taxonomic composition. Therefore, eight nutrient addition experiments were performed with natural phytoplankton communities from Kongsfjorden, Spitsbergen, in June 2015 at the end of the phytoplankton spring bloom period. Phytoplankton biomass and taxonomic composition, growth, PSII characteristics, electron transport rates, and the electron requirement of carbon fixation were measured to investigate (1) the limiting nutrient of phytoplankton growth in Kongsfjorden, (2) the photophysiology under nutrient limited

growth in this Arctic coastal ecosystem, and (3) the effect of nutrient limitation and phytoplankton taxonomic composition on estimates of electron transport in Arctic phytoplankton communities. The results are discussed in the context of photophysiological acclimation in response to environmental conditions and the consequences for phytoplankton primary production and growth in polar regions.

Method

Collection of seawater samples

In June 2015, eight nutrient addition experiments were performed with natural phytoplankton communities from Kongsfjorden, Spitsbergen. Phytoplankton communities were collected at 5 m depth in central Kongsfjorden (79°N, 11°40'E) using a 12-L Niskin bottle. A CTD (SBE 19 plus, Sea-Bird Electronics) profile was made simultaneously to assess depth, temperature, salinity, photosynthetic active radiation (PAR, 400–700 nm), Chl *a* fluorescence and conductivity (Table 1). A detailed description of data processing and water column conditions is described by Van de Poll et al. (in press).

Experimental design

For the nutrient addition experiments, triplicate subsamples (175 mL) of natural phytoplankton communities were incubated for 3 d in a temperature and light controlled setup using polystyrene cell culture flasks (Greiner). Samples used for the incubations were unfiltered and therefore included all grazers present in the natural seawater samples (see Van de Poll et al. in press). In the experimental setup, 20 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ was provided continuously (no dark period) by a 250 W MHNTD lamp (Philips), which closely matched the diurnal cycle in Kongsfjorden in June (Kirk 1994) and a natural PAR spectrum (Kulk et al. 2013). Photoacclimation to the relatively lower irradiance intensity in the experimental setup (Table 1) was thereby established within 24 h (as measured by fast repetition rate fluorometry [FRRF]). Temperature was maintained at $3.5 \pm 0.5^\circ\text{C}$ using a thermostat (Neslab RTE-111) which was similar to in situ conditions at the beginning of June (Table 1). In situ

Table 1. Overview of water column conditions during sampling (5 m depth) of natural phytoplankton communities in Kongsfjorden, Spitsbergen, with the experiment number, date, temperature (T in $^\circ\text{C}$), salinity (S), PAR (daily mean in $\mu\text{mol photons m}^{-2} \text{s}^{-1}$), stratification index ($\Delta\sigma_\theta$ in kg m^{-2}), mixed layer depth (MLD in m), concentration ($\mu\text{mol L}^{-1}$) of NO_3 , NH_4 , PO_4 , and Si, N : P ratio, and Chl *a* concentration (Chl *a* in $\mu\text{g L}^{-1}$). Complete overview of water column conditions is described by Van de Poll et al. (in press).

Experiment	Date	T	S	PAR	$\Delta\sigma_\theta$	MLD	NO_3	NH_4	PO_4	Si	N : P	Chl <i>a</i>
M1	05 Jun 2015	2.72	34.4	196	0.30	15	0.171	0.310	0.052	0.924	9.5	0.776
M2	08 Jun 2015	3.65	34.5	129	0.44	2	0.077	0.205	0.037	0.834	7.7	1.064
M3	11 Jun 2015	2.92	34.0	225	0.34	25	0.189	0.802	0.214	0.442	4.7	0.668
M4	15 Jun 2015	3.66	33.9	164	0.54	8	0.139	0.286	0.054	0.641	8.1	3.146
M5	18 Jun 2015	3.95	34.1	185	0.72	7	0.079	0.273	0.035	0.417	10.3	1.815
M6	22 Jun 2015	5.19	34.2	196	1.16	3	0.043	0.135	0.043	0.377	4.1	0.538
M7	25 Jun 2015	6.41	33.6	138	1.96	2	0.044	0.233	0.021	0.699	13.4	0.774
M8	28 Jun 2015	6.74	33.5	56	2.19	8	0.088	0.264	0.024	1.125	14.8	1.359

temperatures increased later in June, but no obvious effect of lower incubation temperatures on photophysiology was observed in experiment M6–M8 (as measured by FRRf). During the experiments, six different nutrient addition treatments were established: Control (C), added Nitrate (N), added Phosphate (P), added Silicate (Si), added Nitrate and Phosphate (NP), and added Nitrate, Phosphate, and Silicate (NPSi). The C treatment contained in situ nutrient concentrations (no nutrients added) (Table 1). To all other treatments, nutrients were added according to natural concentrations observed at Kongsfjorden during winter (Van de Poll et al. 2016). Therefore, 11.0 μM NO_3 was added to all treatments containing additional N (N, NP, NPSi), 0.7 μM PO_4 was added to all treatments containing additional P (P, NP, NPSi), and 5.0 μM Si was added to all treatments containing additional Si (Si, NPSi). At the beginning ($t = 0$ d) and the end ($t = 3$ d) of the experiment, samples were collected for the analysis of nutrient concentrations ($t = 0$ d only), phytoplankton biomass and species composition, and net phytoplankton growth and photophysiology. Additional measurements of photophysiology at $t = 1$ – 2 d yielded similar results to the end of the experiment ($t = 3$ d) unless otherwise stated.

Nutrient concentrations

Samples for nutrient analysis (5 mL) were collected from seawater samples at $t = 0$ d. Samples were filtered using a 0.2 μm PF membrane filter (Acrodisc Supor®) and stored at 4°C for Silicate and –20°C for all other samples. Inorganic Ammonium (NH_4), Nitrite (NO_2), Nitrate and Nitrite (NO_x), Phosphate (PO_4), and Silicate (Si) were measured using a Traacs 800 autoanalyzer (Bran & Luebbe) according to Murphy and Riley (1962), Helder and De Vries (1979), and Grashoff (1983).

Phytoplankton biomass and composition

Samples for pigment analysis were collected from seawater samples at $t = 0$ d (1500–3000 mL) and at the end of the nutrient addition experiments at $t = 3$ d (130–150 mL) for all incubations. Samples were filtered onto 25 mm ($t = 3$ d) or 47 mm ($t = 0$ d) GF/F filters (Whatman), snap frozen in liquid nitrogen, and stored at –80°C until further analysis. Pigments were quantified using high performance liquid chromatography (HPLC) as described by Van Heukelem and Thomas (2001). In short, filters were freeze-dried for 48 h and pigments were extracted in 3 mL ($t = 3$ d) or 5 mL ($t = 0$ d) 90% acetone (v/v, 48 h, 4°C). Detection of pigments was performed using a HPLC (Waters 2695 separation module, 996 photodiode array detector) equipped with a Zorbax Eclipse XDB-C8 3.5 μm column (Agilent Technologies). Peaks were manually quantified using standards for 19'-but-fucoxanthin, 19'-hex-fucoxanthin, alloxanthin, antheraxanthin (Ant), Chl *a*, chlorophyll *b*, chlorophyll *c*₂, chlorophyll *c*₃, diadinoxanthin (Dd), diatoxanthin (Dt), fucoxanthin, neoxanthin, peridinin, prasinoxanthin, violaxanthin (Vio), and zeaxanthin (Zea) (DHI Lab products). The xanthophyll cycle pigment pool was calculated as the sum of Ant, Dd, Dt, Vio, and Zea per Chl *a* (XC/Chl *a*). The

taxonomic composition of the phytoplankton community was estimated using CHEMTAX (version 1.95) (Mackey et al. 1996). Factor analysis and a steepest descent algorithm based on initial pigment ratios were used to calculate the relative and absolute abundance of dictyochophytes, haptophytes, cryptophytes, dinoflagellates, and prasinophytes as detailed in Van de Poll et al. (in press). Additional microscope analyses were performed for qualitative analysis of the phytoplankton community (see Van de Poll et al. in press).

Phytoplankton growth and photophysiology

Samples for the analysis of phytoplankton net growth and photophysiology were collected daily ($t = 0$ – 3 d) and measured using a FastOcean & Act2 FRRf (Chelsea Ltd.). This technique is based on the underlying principle that energy absorbed by Chl *a* can follow three pathways: energy can be used to drive photosynthesis (photochemical quenching), excess energy can be dissipated as heat (nonphotochemical quenching), or energy can be re-emitted as light (chlorophyll fluorescence) (Maxwell and Johnson 2000). Measuring Chl *a* fluorescence thereby allows for the assessment of various photochemical and nonphotochemical parameters that described the efficiency of PSII. Prior to analysis, all samples (3 mL) were dark adapted for 15 min under temperature controlled conditions. For analysis, single turnover acquisitions consisting of a saturation phase of 100 flashlets on a 2 μs pitch and a relaxation phase of 40 flashlets on a 60 μs pitch were provided using a blue LED excitation source (450 nm). Measured fluorescence transients (mean of 19–20 single turnover acquisitions) were fitted according to the biophysical model of Kolber et al. (1998) using Act2Run software (Chelsea Ltd.) to obtain (1) the minimum fluorescence derived Chl *a* concentration (Chl a_{F0} in $\mu\text{g L}^{-1}$); (2) the maximum quantum yield of PSII (F_v/F_m), i.e., the proportion of absorbed light in PSII that is used for photochemistry; (3) the absorption cross section of PSII at 450 nm ($\sigma_{\text{PSII}(450)}$ in $\text{nm}^2 \text{PSII}^{-1}$), i.e., the physical cross section of PSII that is used for photochemistry; (4) re-opening of closed reaction center II (RCII) (τ_{ES} in μs); (5) PSII connectivity (ρ), i.e., the efficiency of energy transfer from closed to open RCII; and (6) Stern–Volmer normalized NPQ_{NSV} at 700 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$, i.e., the thermal dissipation of excess energy reflecting photoprotective processes as well as damage to the reaction centers of PSII. NPQ_{NSV} was chosen over conventional estimates of NPQ as this approach is more appropriate in comparing samples with varying taxonomic compositions (McKew et al. 2013). Chl a_{F0} was normalized to HPLC derived Chl *a* concentrations and used to estimate net growth rates (μ) by linear regression of natural log-transformed concentrations (3–4 data points). These fluorescence-based growth rates might reflect an overestimation relative to cell count-based growth rates as cellular Chl *a* can increase after relief of nutrient limitation (Geider et al. 1993, 1998; Berges et al. 1996). An index for nutrient limitation for each incubation was derived from the difference in net growth between the C treatment and the other nutrient addition treatments.

Additional samples (3 mL) for the analysis of fluorescence light curves (FLCs) were collected from seawater samples at $t = 0$ d and at the end of the nutrient addition experiments at $t = 3$ d for all incubations. The FLCs consisted of a 16 level light curve (60 s per level) in which 0–1225 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ were provided by white LED light in a temperature controlled FRRf sample head ($3.5 \pm 0.5^\circ\text{C}$). Ideally the provided actinic light would spectrally match the excitation light to derive σ_{PSII} and the effect of a spectral correction is further detailed in the discussion. Chl *a* normalized electron transport rates (ETRs in $\text{mol e}^- \mu\text{g Chl } a^{-1} \text{ h}^{-1}$) were calculated according to Kolber and Falkowski (1993) following Eq. 1:

$$\text{ETR} = E \times \Delta F / F'_v \times \sigma_{\text{PSII}(450\text{nm})} \times n_{\text{PSII}} \quad (1)$$

where E is the irradiance in $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$, $\Delta F / F'_v$ is the effective quantum yield of PSII, $\sigma_{\text{PSII}(450\text{nm})}$ is the absorption cross section of PSII at 450 nm under ambient light in $\text{nm}^2 \text{ PSII}^{-1}$, and n_{PSII} is the number of PSII units per Chl *a* and is derived according to Oxborough et al. (2012) using the Chl *a* concentration ($\mu\text{g L}^{-1}$) obtained by HPLC analysis and the calibration files from the FRRf (Chelsea Ltd.). Units were converted from seconds to hours, nm^2 to m^2 and $\mu\text{mol photons}$ to mol e^- , assuming that one absorbed and delivered photon to RCII leads to one charge separation. ETR curves were then fitted according to Platt et al. (1980) ($r^2 > 0.98$ for all FLCs) to obtain the maximum electron transport rate (ETR_{max} in $\text{mol e}^- \mu\text{g Chl } a^{-1} \text{ h}^{-1}$), the initial slope of the ETR curve (α_{ETR} in $\text{mol e}^- \mu\text{g Chl } a^{-1} \text{ h}^{-1} [\mu\text{mol photons m}^{-2} \text{ s}^{-1}]^{-1}$), and the photoacclimation index of electron transport (E_k in $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$). For samples collected at $t = 0$ d, the electron requirement of carbon fixation ($\Phi_{\text{e,C}}$ in $\text{mol e}^- \text{mol C}^{-1}$) was calculated using the ETR estimates from this study and the carbon fixation measurements reported by Van de Poll et al. (in press). In short, Photosynthesis–Irradiance incubations were performed according to Lewis and Smith (1983) in which subsamples (20 mL) were incubated with $\text{NaH}^{14}\text{CO}_3$ for 3 h at 21 light intensities ranging from 0 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ to 1500 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ (250 W MHNTD lamp, Philips) in a temperature controlled setup. Depth integrated estimates of electron transport and carbon fixation were calculated using vertical Chl *a* profiles, light attenuation, and incident PAR as detailed by Van de Poll et al. (in press), from which $\Phi_{\text{e,C}}$ was obtained. A spectral correction could not be applied without the measurement of the Chl *a* specific absorption coefficient ($a_{\text{ph}}^*(\lambda)$) and the consequences for the interpretation of $\Phi_{\text{e,C}}$ are further detailed in the discussion.

Statistical analysis

Differences between the nutrient treatments were statistically tested by analysis of variance and Tukey HSD post hoc analysis using STATISTICA software (version 13.0, Statsoft). Before analysis, data were tested for normality and homogeneity of variances and log transformed for further statistical

analysis when necessary. Spearman rank correlation analysis was used to test relationships between the photophysiological parameters and the taxonomic composition and nutrient limitation index, while the relationship between ETR_{max} and α_{ETR} was statistically tested by regression analysis. Differences were considered significant when $p < 0.05$.

Results

Nutrient concentrations

Nutrient concentrations in central Kongsfjorden were generally low in June 2015 and negative trends with stratification and temperature were found ($p < 0.05$) (Table 1, Van de Poll et al. in press). At 5 m depth, the most abundant form of nitrogen was NH_4 with concentrations ranging from 0.135 μM to 0.802 μM , whereas NO_3 concentrations ranged from 0.043 to 0.189 (Table 1). PO_4 concentrations ranged from 0.021 μM to 0.214 μM and the N : P ratio was lower than Redfield (16 : 1) and ranged from 4.1 to 14.8 (Table 1). Highest concentrations in N and P were observed on 11 June 2015 (M3). Si concentrations ranged from 0.377 μM to 1.125 μM and were highest at the beginning and end of June 2015 (M1 and M8) (Table 1).

Biomass and taxonomic composition

Phytoplankton biomass in central Kongsfjorden varied between 0.54 $\mu\text{g Chl } a \text{ L}^{-1}$ and 3.15 $\mu\text{g Chl } a \text{ L}^{-1}$ and peaked mid-June at the time of experiment M4 (15 June 2015) (Table 1). Chl *a* concentrations at 5 m depth showed no clear trend with water column conditions, but depth-integrated Chl *a* was positively related to stratification and temperature (Van de Poll et al. in press). The phytoplankton community was dominated by dictyochophytes (76–96%) at the beginning of June during experiment M1–M5 ($t = 0$ d, Fig. 1). At the start of experiment M6–M8, the contribution of

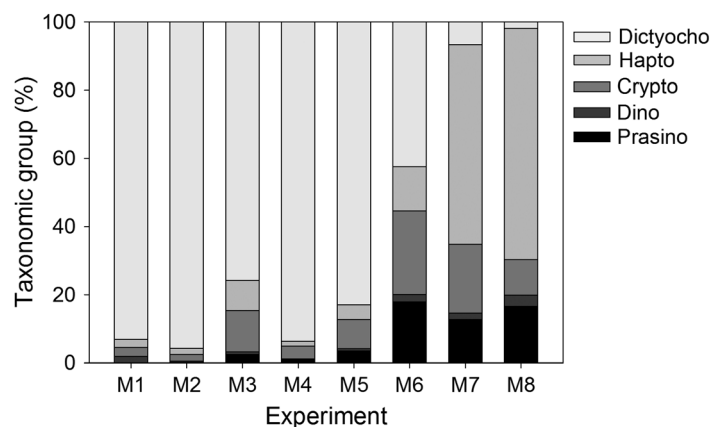


Fig. 1. Taxonomic composition of the phytoplankton community in central Kongsfjorden at the beginning of the nutrient addition experiments ($t = 0$ d) with the relative contribution (%) of total biomass of dictyochophytes (Dictyochlo), haptophytes (Hapto), cryptophytes (Crypto), dinoflagellates (Dino), and prasinophytes (Prasino).

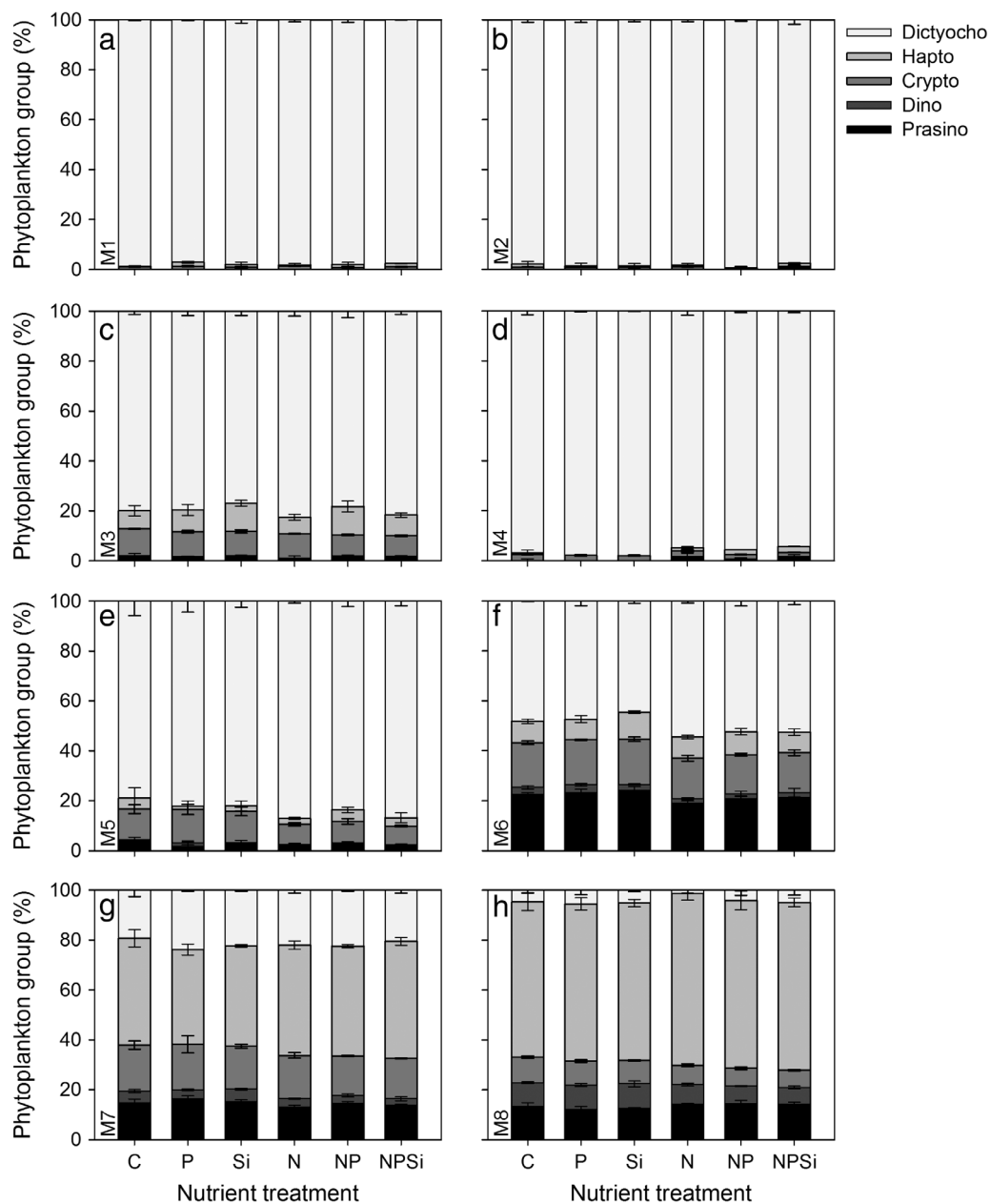


Fig. 2. Mean (\pm standard deviation, $n = 3$) taxonomic composition of natural phytoplankton communities incubated without additional nutrients (C) and additional P, Si, N, NP, and NPSi for (a) experiment M1, (b) experiment M2, (c) experiment M3, (d) experiment M4, (e) experiment M5, (f) experiment M6, (g) experiment M7, and (h) experiment M8. The relative contribution (%) of total biomass is given for dictyochophytes (Dictyocho), haptophytes (Hapto), cryptophytes (Crypto), dinoflagellates (Dino), and prasinophytes (Prasino).

dictyochophytes decreased and the phytoplankton community was dominated by prasinophytes (13–18%), cryptophytes (10–24%), and haptophytes (13–68%). The changes in taxonomic composition were associated with changes in phytoplankton cell size, which decreased from 10–15 μm to 2–5 μm over time (Van de Poll et al. in press). No significant changes in taxonomic composition of the phytoplankton communities were observed during the course of the nutrient addition experiments (Fig. 2).

Growth

Fluorescence-based net growth rates in the nutrient addition experiments decreased over the course of June and ranged between $-0.15 \pm 0.015 \text{ d}^{-1}$ (Si treatment M5) and $0.43 \pm 0.044 \text{ d}^{-1}$ (P treatment M1) (Fig. 3a). In the first two experiments (M1 and M2), net growth rates were similar between the different nutrient addition treatments. In experiment M3, higher net growth rates were observed after the addition Si, NP, and NPSi compared to C, P, and N ($p < 0.001$). From mid-June onwards

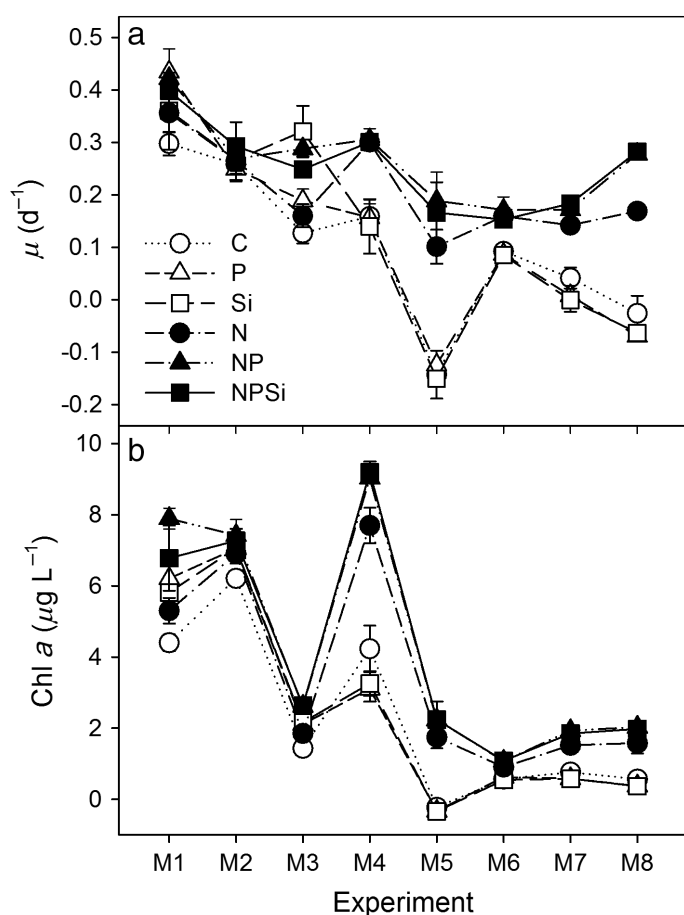


Fig. 3. Mean (\pm standard deviation, $n = 3$) (a) net growth rate (μ) and (b) increase in Chl *a* concentration throughout the incubation experiments for natural phytoplankton communities incubated without additional nutrients (C) and additional P, Si, N, NP, and NPSi. Net growth rates are based on the increase of minimum fluorescence obtained by FRRf.

(M4–M8), the addition of nitrogen (N, NP, and NPSi) resulted in higher net growth rates compared to treatments without additional nitrogen (C, P, and Si) ($p < 0.001$). Moreover, the addition of NP and NPSi resulted in higher net growth rates compared to the addition of only N in the final experiment M8 ($p < 0.001$). Fluorescence-based net growth was associated with an increase in Chl *a* throughout the experiments (Fig. 3b) with highest biomass accumulation observed after addition of nitrogen in experiment M4 ($9.1 \pm 0.22 \mu\text{g Chl } a \text{ L}^{-1}$).

Photophysiology

F_v/F_m of the phytoplankton communities collected in central Kongsfjorden varied between 0.31 ± 0.007 (M3) and 0.53 ± 0.005 (M4) ($t = 0$). Within 24 h after the start of the experiments, F_v/F_m increased to values observed at the end of the incubations ($t = 3$ d). No significant differences in F_v/F_m were observed between nutrient treatments at the end of experiments M1–M7 (Fig. 4a). In experiment M8, the F_v/F_m was 7.1–13.5% lower in the N, NP, and NPSi treatments

compared to the C, P, Si treatments ($p < 0.001$). $\sigma_{\text{PSII}(450\text{nm})}$ of the phytoplankton communities collected at $t = 0$ d varied between $5.14 \pm 0.250 \text{ nm}^2 \text{ PSII}^{-1}$ (M3) and $6.33 \pm 0.199 \text{ nm}^2 \text{ PSII}^{-1}$ (M8) and changed according to different nutrient treatments during the course of the experiments. No significant differences in $\sigma_{\text{PSII}(450\text{nm})}$ were observed between nutrient treatments for experiments M1–M3 and M7 (Fig. 4b). In experiments M4–M6 and M8, the addition of nitrogen (N, NP, and NPSi) resulted in lower $\sigma_{\text{PSII}(450\text{nm})}$ compared to treatments without additional nitrogen (C, P, and Si) ($p < 0.05$). τ_{ES} varied between $2546 \pm 29 \mu\text{s}$ (M5) and $3936 \pm 732 \mu\text{s}$ (M8) at the start of the experiments ($t = 0$ d) and increased up to 10-fold during experiments M7 and M8. No differences in τ_{ES} were observed between the different nutrient treatments in experiments M1–M6 (Fig. 4d). In experiment M7, τ_{ES} was highest in the C treatment, followed by the N and P treatments ($p < 0.001$). In experiment M8, the addition of nitrogen (N, NP, and NPSi) resulted in higher τ_{ES} compared to treatments without additional nitrogen (C, P, and Si) ($p < 0.001$). ρ decreased from experiment M4 onwards (except $t = 0$ d, M3) and values ranged from 0.08 ± 0.019 (N, M7) to 0.45 ± 0.015 (P, M4) (Fig. 4d). No clear differences in ρ were observed between the different nutrient treatments. Initial NPQ_{NSV} of the phytoplankton communities collected in central Kongsfjorden varied between 2.82 ± 0.380 (M8) and 4.70 ± 0.209 (M3) ($t = 0$) and levels decreased to values observed at the end of the incubations ($t = 3$ d) within 24 h. At $t = 3$ d, NPQ_{NSV} varied between the experiments with highest levels observed during experiment M4 (ranging from 2.81 ± 0.50 to 3.52 ± 0.40) (Fig. 4e). No differences in NPQ_{NSV} between nutrient treatments were observed during experiment M1 and M3–M8. In experiment M2, NPQ_{NSV} was higher in the Si treatment compared to the other treatments ($p < 0.05$). $\text{XC}/\text{Chl } a$ of the phytoplankton communities collected at $t = 0$ d varied between 0.09 (M2) and 0.15 (M4) and decreased during the experiments (Fig. 4f). At $t = 3$ d, no significant differences in $\text{XC}/\text{Chl } a$ between the different nutrient treatments were observed in the experiments M1–M3 and M6–M8. In experiments M4 and M5, the addition of nitrogen (N, NP, and NPSi) resulted in lower $\text{XC}/\text{Chl } a$ compared to treatments without additional nitrogen (C, P, and Si) ($p < 0.05$). Variations in the PSII fluorescence parameters were correlated to taxonomic composition (Table 2). Variations in $\sigma_{\text{PSII}(450\text{nm})}$ were also correlated to nutrient limitation, but this relationship was not observed for the other parameters (Table 2).

Electron transport rates

ETR_{max} increased during the incubation in experiment M1–M4 and M6, but remained similar to initial rates at $t = 0$ d in experiment M5, M7, and M8 ($p < 0.001$). No differences in ETR_{max} were observed between nutrient treatments in experiments M1 and M3–M8 (Fig. 5a). In experiment M2, ETR_{max} was higher in phytoplankton communities incubated with additional phosphate (P, NP, NPS) compared to the other nutrient treatments (C, Si, N)

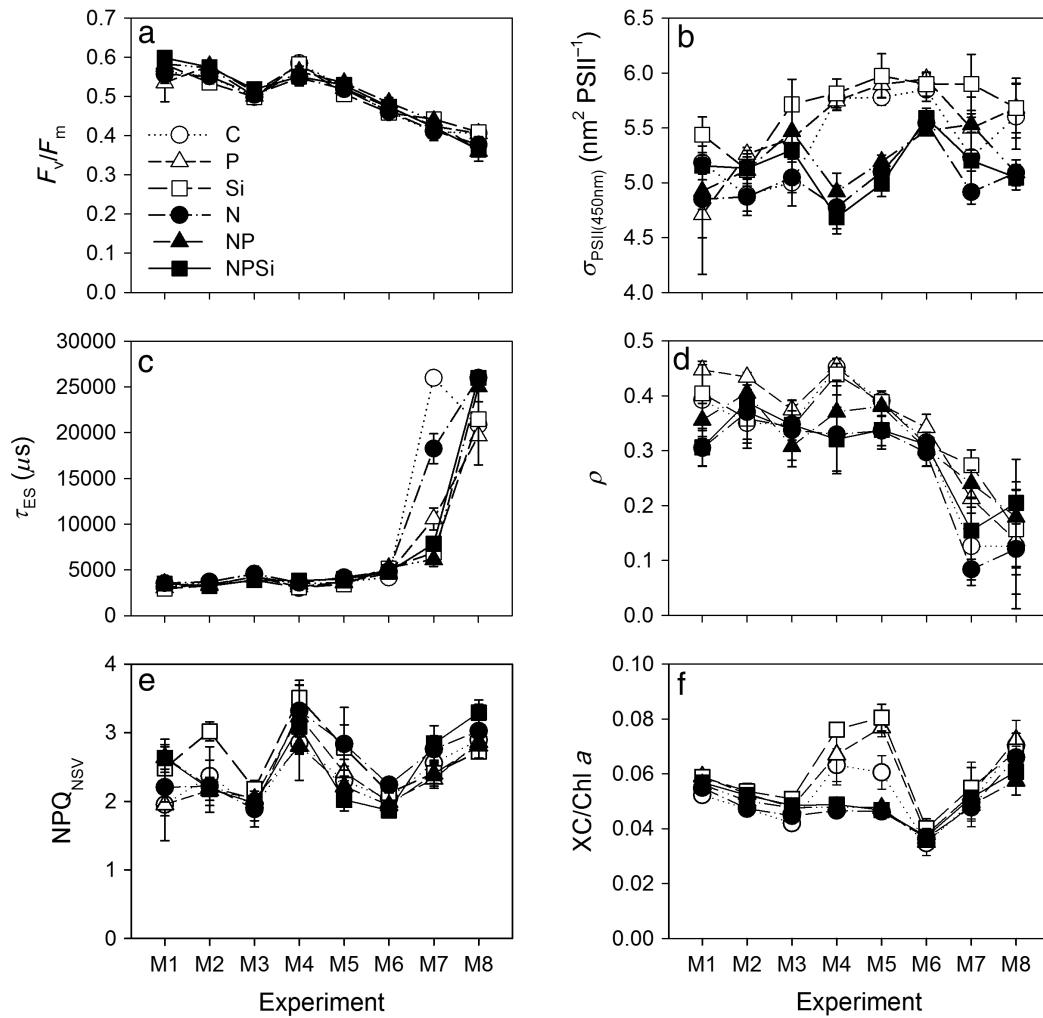


Fig. 4. PSII fluorescence parameters with the mean (\pm standard deviation, $n = 3$) (a) maximum quantum yield of PSII (F_v/F_m), (b) absorption cross section of PSII ($\sigma_{\text{PSII}(450\text{nm})}$), (c) reopening of closed RCII (τ_{ES}), (d) PSII connectivity (ρ), and (e) NPQ_{NSV} ; and phytoplankton pigments with the mean (\pm standard deviation, $n = 3$) (f) ratio of xanthophyll cycle pigments per chlorophyll a (XC/Chl a) for natural phytoplankton communities incubated without additional nutrients (C) and additional P, Si, N, NP, and NPSi.

Table 2. Spearman rank correlation coefficients between the taxonomic groups and nutrient limitation index (difference in growth between control and nutrient treatments), and the maximum quantum yield of PSII (F_v/F_m), absorption cross section of PSII ($\sigma_{\text{PSII}(450\text{nm})}$), reopening of closed RCII (τ_{ES}), PSII connectivity (ρ), nonphotochemical quenching (NPQ_{NSV}), xanthophyll cycle pigments per Chl a ratio (XC), maximum electron transport rate (ETR_{max}), initial slope of the ETR curve (α_{ETR}), and photoacclimation index (Ek) measured at the end of the nutrient addition experiments ($t = 3$ d). Significant differences are indicated by * for $p < 0.05$ and ** for $p < 0.001$.

	F_v/F_m	$\sigma_{\text{PSII}(450\text{nm})}$	τ_{ES}	ρ	NPQ_{NSV}	XC	ETR_{max}	α_{ETR}	Ek	$\Phi_{e,C}$
Dictyochophytes	0.928**	-0.281**	-0.873**	0.747**	0.799**	0.063	0.864**	0.921**	0.218	-0.697**
Haptophytes	-0.892**	0.163	0.869**	0.760**	-0.785**	-0.100	-0.788**	-0.877**	-0.116*	-0.660**
Cryptophytes	-0.721**	0.497**	0.633**	0.478**	-0.737**	-0.321**	-0.728**	-0.743**	-0.247	0.637**
Dinoflagellates	-0.720**	0.199*	0.705**	0.675**	-0.632**	0.145	-0.801**	-0.744**	-0.460**	0.310
Prasinophytes	-0.806**	0.328**	0.752**	-0.636**	-0.800**	-0.343**	-0.763**	-0.801**	-0.190	0.695**
Nutrient limitation	-0.075	-0.508**	0.110	-0.150	-0.174	0.013	0.013	-0.096	0.305*	0.115

($p < 0.05$). α_{ETR} ranged from $6.71 \times 10^{-4} \pm 5.68 \times 10^{-5}$ ($t = 0$, M7) to $6.12 \times 10^{-3} \pm 2.43 \times 10^{-4}$ (P, M2) $\text{mol e}^- \mu\text{g Chl } a^{-1} \text{ h}^{-1}$ ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$) $^{-1}$ and was positively related to ETR_{max}

($p < 0.001$, $r^2 = 0.8675$, Fig. 5b). As a consequence, Ek remained relatively constant throughout the experiments and was on average $133 \pm 23.8 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ (data not shown).

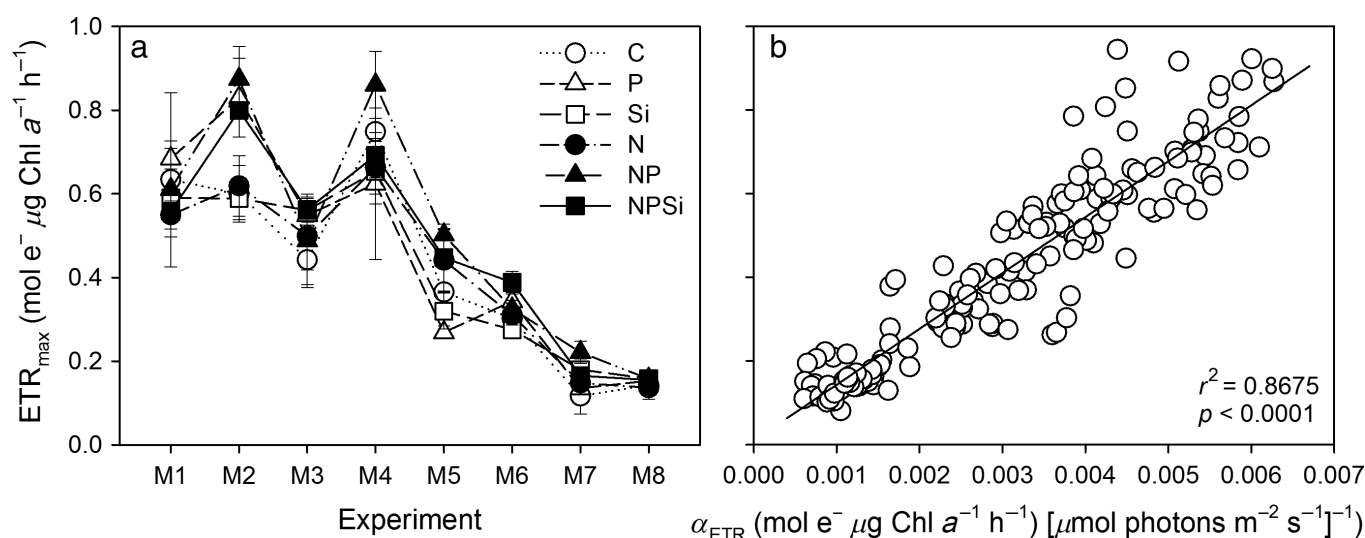


Fig. 5. Electron transport rates with (a) mean (\pm standard deviation, $n = 3$) ETR_{max} for natural phytoplankton communities incubated without additional nutrients (C) and additional P, Si, N, NP, and NPSi and (b) the relationship between ETR_{max} and the initial slope of the ETR curve (α_{ETR}) for all incubations during the nutrient addition experiments. Data presented in (b) were fitted by linear regression analysis ($r^2 = 0.8675$, $p < 0.001$).

Variations in ETR_{max} and α_{ETR} were correlated to taxonomic composition (Table 2), but not to nutrient limitation. The electron requirement of carbon fixation ($\Phi_{e,C}$) of natural phytoplankton communities in Kongsfjorden varied between $2.8 \pm 0.15 \text{ mol e}^- \text{ mol C}^{-1}$ and $8.3 \pm 1.60 \text{ mol e}^- \text{ mol C}^{-1}$ at the start ($t = 0 \text{ d}$) of experiment of M1, M2, M4, and M5 (Fig. 6). At the start of experiment M3 and M6–M8, the $\Phi_{e,C}$ was significantly higher with values ranging from 16.7 ± 2.09 (M6) $\text{mol e}^- \text{ mol C}^{-1}$ to 23.1 ± 4.14 (M3) $\text{mol e}^- \text{ mol C}^{-1}$ ($p < 0.001$). Variations in $\Phi_{e,C}$ were correlated to in situ NO_3 concentrations (Spearman's $\rho = -0.8144$, $p < 0.001$), taxonomic composition (Table 2), and F_v/F_m , τ_{ES} , and ρ (Spearman's $\rho = -0.7381$, -0.9048 , -0.9286 , respectively, $p < 0.05$).

Discussion

Kongsfjorden is situated in a region that is strongly influenced by sea ice formation (Kortsch et al. 2012) and melting of marine terminating glaciers (Luckman et al. 2015). Meltwater induced density stratification thereby initiates the phytoplankton bloom in spring, while depletion of nutrients from surface waters is believed to be a driving factor in phytoplankton succession during summer (Strom et al. 2006; Iversen and Seuthe 2011; Van de Poll et al. in press). This study showed that the phytoplankton community in central Kongsfjorden was nitrate limited from mid-June onwards, as evident from the increased net growth rates and biomass accumulation observed after the addition of nitrate and/or nitrate in combination with phosphate and silicate (Fig. 3). Similar observations were made in Kongsfjorden and other Arctic coastal regions where the addition of nitrogen in combination with other nutrients led to enhanced growth rates (Strom et al. 2006; Larsen et al. 2015). In the present study, the addition of both nitrate and phosphate

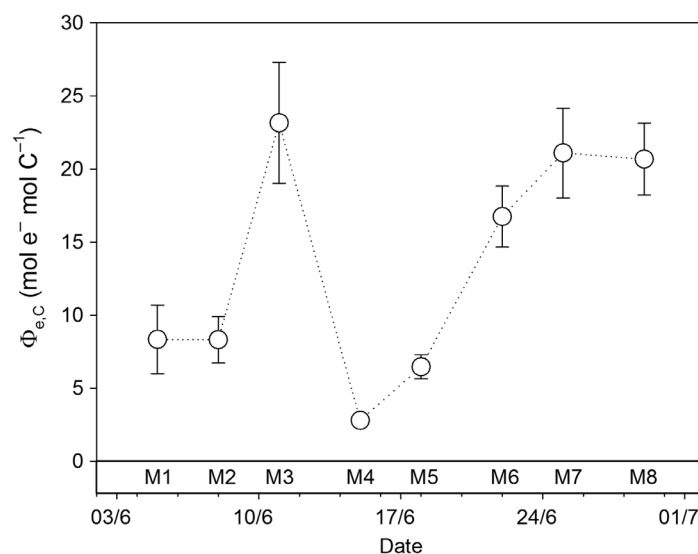


Fig. 6. Mean (\pm standard deviation, $n = 3$) electron requirement for carbon fixation ($\Phi_{e,C}$) at the start of each nutrient addition experiment ($t = 0 \text{ d}$). Measurements were performed with phytoplankton community samples from central Kongsfjorden (open circles) collected at 5 m depth.

led to higher net growth rates toward the end of June compared to those observed after addition of nitrate only. This could indicate that co-limitation by both nutrients occurred or phosphate limitation was induced after the addition of nitrate (Moore et al. 2008). With an increase in in situ nitrogen concentrations and N : P ratios toward the end of June, co-limitation of phytoplankton growth by nitrate and phosphate seems plausible, but phosphate limitation after the addition of nitrate could not be excluded. Silicate limitation was observed on one occasion earlier in June (M3), which coincided with relatively low in situ silicate concentrations and was likely associated with the

dominance of dictyochophytes (i.e., silicoflagellates) (Van de Poll et al. in press). It has previously been suggested that multnutrient limitation of phytoplankton growth has the potential to increase phytoplankton community diversity with subsequent consequences for other trophic levels and overall ecosystem functioning (Larsen et al. 2015; Browning et al. 2017).

The onset of nitrate limitation was followed by a pronounced change in phytoplankton taxonomic composition with a shift in dominance from dictyochophytes to a mixed community with haptophytes, cryptophytes, and prasinophytes in central Kongsfjorden (Figs. 1, 2) (also see Van de Poll et al. in press). Previous studies have shown similar changes in taxonomic composition of phytoplankton communities in coastal Arctic fjords where diatoms dominate during the phytoplankton bloom and haptophytes, cryptophytes, and prasinophytes thrive under post-bloom conditions (Hodal et al. 2012; Piquet et al. 2014; Van de Poll et al. 2016). This shift in species composition and associated changes in community cell sizes has often been related to low nutrient availability with smaller species having a competitive advantage due to high surface-area-to-volume ratios (Raven 1998; Li et al. 2009; Lindemann et al. 2016). Earlier observations also confirm the absence of diatoms in Kongsfjorden later in the season when availability of silicate is low (Piquet et al. 2014; Larsen et al. 2015). While previous short-term incubation studies in the Arctic have shown that specific phytoplankton size classes respond differently to nutrient addition, differences in taxonomic composition during these experiments were not assessed (Strom et al. 2006; Larsen et al. 2015). Despite the changes in taxonomic composition observed in central Kongsfjorden during June, the present study showed that short-term nutrient additions (3 d) can lead to increased phytoplankton biomass without allowing sufficient time to alter the taxonomic composition of the phytoplankton community. While changes in photophysiology are often difficult to observe in natural phytoplankton communities due to the combined effects of environmental conditions and phytoplankton community structure (Suggett et al. 2009), the constant taxonomic composition during the short-term incubations of this study allowed for the assessment of the effects of nutrient limitation and taxonomic composition on photophysiology and electron transport rates.

Earlier observations in the Arctic related variations in the maximum quantum yield of PSII and the absorption cross section of PSII to different light and/or nutrient conditions, but no clear relationship with phytoplankton biomass or taxonomic composition was observed (Erga et al. 2014; Falkowski et al. 2017; Schuback et al. 2017). In the present study, the changes observed in PSII photophysiology were not directly associated with the relief of nutrient limitation, except for the absorption cross section of PSII which decreased after nitrate addition toward the end of June (Fig. 4). This is in accordance with the general observation that the absorption cross section of PSII increases during nutrient starvation and/or

limitation in laboratory experiments and natural phytoplankton communities across the open oceans (Kolber et al. 1988; Suggett et al. 2009; Schuback et al. 2015). Nitrogen starvation and/or limitation can thereby lead to a reduction in the cellular density of PSII reaction centers, but an increase in the effective size of the PSII antennae (Kolber et al. 1988; Beardall et al. 2001). In mid-June, this might have been associated with a reduction in cellular Chl *a* and subsequent increase in the relative concentration of photoprotective pigments (Geider et al. 1993, 1998; Berges et al. 1996). In contrast to the absorption cross section of PSII, the changes in maximum quantum yield of PSII, reopening of closed RCII, PSII connectivity, and nonphotochemical quenching did not vary between the different nutrient treatments (Fig. 4), suggesting that species composition rather than nutrient limitation played a more important role in the variation observed in PSII photophysiology between the different experiments. Earlier laboratory studies with Antarctic phytoplankton species showed that PSII connectivity and PSII turnover rates were not affected by CO₂ concentration or light availability, but was different among various Antarctic phytoplankton species with lowest values found in the haptophyte *Phaeocystis antarctica* (Trimborn et al. 2014). The nutrient limited community dominated by haptophytes in the present study showed similar photophysiology with lower PSII efficiency associated with low connectivity between reaction centers and slow reopening of closed reaction centers. This is believed to reflect variations in photoprotection with diatoms and dictyochophytes efficiently redistributing light energy with high connectivity between PSII reaction centers leading to the promotion of nonphotochemical quenching, while changes in the re-oxidation of closed PSII reaction centers may prevent photodamage in haptophytes (Ihnken et al. 2011; Trimborn et al. 2014; Schuback et al. 2017).

Variations in electron transport rates and the electron requirement of carbon fixation in polar phytoplankton communities have previously been related to changes in photophysiology in response to environmental conditions (Cheah et al. 2011; Hancke et al. 2015; Schuback et al. 2015, 2017). While estimates of electron transport rates were closely linked to functioning of PSII in the present study (Fig. 5), this was driven by changes in taxonomic composition rather than a direct effect of nutrient availability or nutrient limitation. The initial slope and maximum rate of electron transport were thereby tightly coupled resulting in a relative constant photoacclimation index independent of taxonomic composition. Coupling of the initial slope and maximum rate of photosynthesis at the level of basic photochemistry is constrained by variations in the PSII : PSI ratio (Behrenfeld et al. 2004) and has previously been observed at higher latitudes (Harrison and Platt 1986; Behrenfeld et al. 2004; Schuback et al. 2017). In the present study, the electron requirement of carbon fixation increased toward the end of June (Fig. 6), indicating that alternative electron pathways

were present in the nutrient limited phytoplankton communities in Kongsfjorden. The observed electron requirement of carbon fixation were within the range reported before and close to the theoretical minimum of 4–6 mol e⁻ mol C⁻¹ at the beginning of June (Lawrenz et al. 2013; Hancke et al. 2015). Yet, the values reported in the present study might have been underestimated by ~ 30% as accurate comparison of the electron requirement of carbon fixation relies on a spectral correction of the absorption cross section of PSII and incubator light spectra (Moore et al. 2006; Hancke et al. 2015). It has previously been suggested that alternative electron pathways play an important role in the response of Arctic phytoplankton communities to high irradiance intensities and this could explain the variation in the electron requirement of carbon fixation (Hancke et al. 2015; Schuback et al. 2015, 2017). Biochemical processes, such as photorespiration, chlororespiration, and nutrient assimilation can thereby affect the relationship between electron transport and carbon fixation (Badger et al. 2000; Beardall et al. 2001; Mackey et al. 2008). With a direct relationship between in situ nitrogen concentrations and the electron requirement of carbon fixation (also see Schuback et al. 2017), the present study suggests that energy derived from the light reactions of photosynthesis may be used for the uptake of nutrients at the expense of carbon fixation (Falkowski and Stone 1975; Beardall et al. 2001). An alternative energy pathway is further supported by the similar observations in PSII photophysiology and electron transport rates after nitrate addition while net growth rates increased in the N, NP, and NPSi incubations at the end of June, indicating that more energy generated in PSII was allocated toward (carbon fixation and) growth after relief of nutrient limitation.

Conclusions

Changes in photophysiology are often difficult to observe in natural phytoplankton communities, with the variability in photophysiology driven by both light and nutrient availability and phytoplankton biomass and taxonomic composition. The nutrient addition experiments in this study allowed for a detailed assessment of photophysiology after relief of nutrient limitation and strong relationships with species composition rather than photophysiological acclimation to nutrient limitation were observed. The phytoplankton community in central Kongsfjorden became nitrate limited from mid-June onwards and the onset of nitrate limitation was followed by a pronounced change in taxonomic composition with a shift in dominance from dictyochophytes to haptophytes and a decrease in phytoplankton cell size. The community dominated by dictyochophytes was characterized by high PSII efficiency with relatively high electron transport rates that were efficiently used for carbon fixation, resulting in high net growth rates. While the taxonomic composition of the phytoplankton community

changed with the onset of nutrient limitation, marked changes in PSII photophysiology were observed with decreasing efficiencies, lower connectivity between reaction centers and slower turnover rates. Simultaneously, alternative electron requirements downstream of PSII became more important thereby reducing carbon fixation and eventually growth. The decoupling between electron transport and carbon fixation is thereby likely related to utilization of electrons to cover the energy requirement for nutrient uptake.

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Conflict of Interest

None declared.

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